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Reconsideration of three Odonata taxa described by A.N. Bartenev from the same place in West Caucasus

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Abstract. *Enallagma cyathigerum* var. *rotundatum* Bartenef, 1929, *Leucorrhinia circassica* Bartenef, 1929, and *Aeschna juncea* var. *atshischgho* Bartenef, 1929, were described by A.N. Bartenev (= Bartenef) in three papers published in 1929 and 1930. Their type locality was the same highland lake group near Krasnaya Polyana Town in West Caucasus, Russia, presently known as the Khmelevskie Lakes. Their type series most probably no longer exist. Topotypes of the two former taxa obtained in 2008 and 2013, respectively, were examined as well as a specimen supposedly of the third taxon, collected 36 km from the type locality. Based on these specimens, *E. cyathigerum rotundatum* is concluded to be a valid subspecies and the senior subjective synonym of *Enallagma risi* Schmidt, 1961, and *L. circassica* to be a junior subjective synonym of *Leucorrhinia dubia* (Vander Linden, 1825). The status of *A. juncea atshischgho* remains unresolved. Re-evaluation of available knowledge of the Palaearctic *Enallagma* spp. suggested downgrading *Enallagma deserti* (Selys, 1879) to the subspecies, *E. cyathigerum deserti*.

Further key words. Dragonfly, damselfly, junior subjective synonym, senior subjective synonym, subspecies

Introduction

General

The distinguished Russian odonatologist, Andrey Nikolaevich Bartenev (1882–1946), working during the first third of the 20th century, was the author of 101 publications (Husainova & Belyshev 1971) and, according to counts based on Bridges (1994), 64 available species group names of Odonata. Of these, only 17 are currently considered valid, 12 as species and five as subspecies; these figures are not precise since ranks of some are still considered equivocal. With very few exceptions, their type specimens were lost

(Medvedev *et al.* 2013). The two latter figures do not take into account three taxa, *Enallagma cyathigerum* var. *rotundatum* Bartenef, 1929, *Leucorrhinia circassica* Bartenef, 1929, and *Aeschna juncea atshischgho* Bartenef, 1929 (note the incorrect generic name spelling »*Aeschna*« used in the original description, but no brackets at the authority according to ICZN Art. 51.3.1), described from the same locality in the Caucasus (Bartenef 1929a, b, 1930), which for a long time were repeatedly supposed to be synonyms (*e.g.*, Kosterin 2004; Kosterin *et al.* 2004; Boudot & Kalkman 2015; Malikova & Kosterin 2019; Onishko & Kosterin 2021) but have not yet been considered in detail. This paper clarifies the status of the two former taxa through examination of topotypic specimens. The third taxon is only briefly discussed because of the lack of topotypes.

The spelling of this author's surname Бартенев with Latin letters needs clarification. When transliterated from Russian to English, it is 'Bartenev' – the Romanised spelling that will be used here – while in other languages it is variably transliterated as either 'Bartenev' or 'Bartenef'. Among his papers considered here, he used both transliterations; (Bartenev 1925) and (Bartenef 1929a, b), while Bartenef (1930) has a German summary but does not give the author's surname in Roman letters. I refer to the latter as 'Bartenef' as well, given his use of this form in other papers with a German summary.

Original descriptions

Enallagma cyathigerum var. *rotundatum* and *L. circassica* were described by Bartenef (1929a, 1930) twice, in 1929 in German and in 1930 in Russian. Both papers use the formulae »var. nov.« for the former and »sp. nov.« for the latter. Naturally, the names proposed in the German paper (Bartenef 1929a) are of priority having been published a year earlier, while those proposed in the Russian paper (Bartenef 1930) are at the same time their junior homonyms and junior objective synonyms. All world catalogues of Odonata mentioned these names with the correct year 1929. The International Code of Zoological Nomenclature (ICZN 1999: Art. 45.6.4) regards a name proposed for a variety before 1961 (unless explicitly infra-subspecific) as subspecific, so the name *rotundatum* should be considered as proposed at the subspecific rank, as *E. cyathigerum rotundatum* Bartenef, 1929.

Aeshna juncea atshischgho was also described twice, in two papers published in the same year: once in German (Bartenef 1929a), as »*Aeschna juncea* var. *atshischgho* var. nov.«, and in a paper in Russian devoted to the *Aeshna juncea* and *A. clepsydra* species groups in the Palaearctic (Bartenef 1929b), as »*Aeschna juncea atshischgho* ssp. n.«. At the end of the text devoted to this taxon in Bartenef (1929b: 52) we also read the following: »while we give the form ... the naming *A. juncea atshischgho* Bart, 1929« (translated from Russian), which could be interpreted as a reference to an earlier published description. However, the reference list contains neither the entry Bartenef (1929a) nor any other of the papers he published that year. Therefore, his formulations did not mean anything and he just found it useful to again describe the taxon twice in different languages. The respective precedence of the two 1929 papers (Bartenef 1929a, b) is unclear, but at least we are sure about 1929 as the year of description. Both papers proposed the new taxon in a subspecific rank, even if described as a variety (ISZN Art. 45.6.4). This taxon was not redescribed in Bartenef (1930), where it was mentioned as »*Aeschna juncea atshischgho* Bart.« and where only ecological information was provided without description or illustrations.

Type localities and type series

Bartenef (1929a: 54) reported the type locality and type series of *L. circassica* in brief: »Seen auf dem Berge Atshischgho (2 365 m über der Meeresfläche), 22. – 23. VII. 1928, teils in coitu, viele Exemplare; 5. VIII. 1929, viele Exemplare« (»lakes at the Achishkho [in English transliteration] Mountain (2 365 m a.s.l.), 22.–23. VII. 1928, partly in copula, many individuals; 5. VIII. 1929, many individuals«). As follows from Bartenef (1930), the elevation provided was that of the mountain top rather than of the lakes, which lie at elevations from 1 700 to 1 779 m a.s.l.

In his subsequent major work on Odonata of the West Caucasus, Bartenef (1930: 6) provided a very detailed description of this locality in Russian (the original style is retained as possible in the translation): »19. Lakes on M[ount] Achishkho (the summit of Achishkho is at 2 365 m a.s.l.), obviously not higher than 2 000 m a.s.l. There is quite a big series of lakes, some of which have a peaty nature. An exact topographic description of the terrain and lakes is missing. The lakes lack names. We will designate their №№,

counted from the Greek balagan [the latter word in this region refers to an unheated shepherd's hut (Valeriy Brinikh pers. comm.)], to which a straight path goes to Achishkho from Krasnaya Polyana (other than that along the Beshenka River). The lake group No. 1: there are 5 lakes in total, of which 3 ones are mossy. Dragonflies were caught mostly at the lake near the balagan. [It is] somewhat polluted, not mossy, with a boggy western (not precisely) corner. Dimensions are about 300 m in diameter. Lake [group] No. 2 are a type of pool left over from rain. Dragonflies are absent. Lake No. 3 of the same size as the lake at the balagan (of group No. 1); with forest around, half-flowing, few boggy places. Lake No. 4 of a pure mossy character, almost completely covered with moss, open water almost absent. Dragonflies are absent. Lake No. 5 is situated higher than the previous one, also of a mossy character, sharply [sic] overgrown; lies in an open place; there are bushes and trees not far on slopes. Lake No. 6. The size similar to that of the lake at the balagan. The lake is 1 ½ m deep. [It is] somewhat overgrown around. The lake richest in dragonflies. Lake No. 7. Immediately behind lake No. 6, strongly overgrown, mossy. Dragonflies are very few«. There is also the following footnote: »Shikleev (Proc. of the North Cauc. Assoc. Sci. Res. Inst. Rostov, 1929, No. 69, p. 9–10) designates these lakes as follows: he calls our lake No. 1 "The pond at the balagan, the water body No. 4."; lake No. 3 – "the water body – depression No. 3"; lake No. 4 – "the water body No. 6"; lake No. 5 – "the water body – depression No. 2"; lake No. 6 – "water body No. 10"; lake No. 7 – "water body – depression No. 1"«. I failed to find the mentioned publication by Shikleev. Bartenev created some confusion by his different numbering of the lakes, nevertheless I will use his system below.

The studied specimens of *L. circassica* were enumerated in Bartenef (1930: 19) more precisely as follows: »Mountain Achishkho, lake No. 1, 22 July 1928, several specimens; lake No. 3, 23 July 1928, many spec., *in coitu*; lake No 6, 23 July 1928, several spec. partly *in coitu*«. Hence, the actual size of the type series remained unknown even after the more detailed 1930 paper. No specimens of 05.viii.1929, mentioned in Bartenef (1929a), were included in the list of specimens studied but in habitat notes, the following information is provided: »So far the species is found only at 3 lakes on Mt Achishkho. As with other species of the genus *Leucorrhinia*, it flies at non-flowing water bodies. It was found at lake No. 1 only at its western corner, overgrown with

low sedge, where the species flew low over the water, where it was difficult to get because of the viscosity of the bottom. At lake No. 3 it flew somewhat higher above the water, flew off from water, rested on sunny lying tree trunks, and several times landed on packs mounted on our horse while it was standing on the bank waiting for us. At lake No. 5 the species was most numerous, flew over sedges or almost inside sedges, landing on them. Pairs *in coitu* flew off the lake and landed on nearby bushes. At lake No. 6, the species was low in number, but pairs *in coitu* also flew. 10–12 August 1927 the species was absent on Mt Achishkho, while on 5 August 1929 it still flew there; this gives reason to suppose that it disappears not later than the beginning of August«.

The type series of *E. cyathigerum rotundatum* was mentioned by Bartenef (1929a: 64) as follows: »Seen auf dem Berge Atshischgho. 22.–23. VII. 1928, ♂♂ und 1 ♀« [»Lakes on Mt Achishkho. 22.–23. VII. 1928, ♂♂ and 1 ♀«], while Bartenef (1930: 63) provided more detail: »Mount Achishkho, l[ake]. No. 6, 23 July 1928, males. – Mount Achishkho, l. No. 1, 22 July 1928, 1 male and 1 female«. The actual number of male syntypes remained unknown again.

Bartenef (1929a: 57–58) communicated the type locality and collecting dates of *A. juncea atshischgho*, but not the number and sex of specimens, as follows: »Seen am Berge Atshischgho in der Umgebung von Krasnaja Poljana (50 km von Adler), 12–13. IX. 1926; 10–12. VIII. 1927; 22–23.VII. 1928; 5. VIII. 1929« [»Lakes at Mount Atchishkho in the vicinity of Krasnaya Polyana (50 km from Adler), 12–13. IX. 1926; 10–12. VIII. 1927; 22–23.VII. 1928; 5. VIII. 1929«], but the characters of both sexes were described. Bartenef (1929b: 51) mentioned just »males and females from the Achishkho and Pseashkho Mountains« and later »there are males and females [represented] by several specimens«. The name Pseashkho appears here for the first time, but this is the mountain situated 20.6 km east of Mt Achishkho, so the same place was actually considered. Bartenef (1930) again provided more specific topographic information but rather on individuals observed than specimens collected, as follows: »Mount Achishkho, l[ake] No. 1 at the balagan, 12 September 1926, only males were flying; 10 August 1927, 2 males; 22–23 July 1928, males and females *en masse*, coitus and oviposition *en masse*. – The same place, l No. 3, 10 August 1927, a males; 23 July 1928, several spec. – The same place, l No. 5, 12 August 1927; 1 male and 1 female, 23 July 1928, several spec. – The same place, l No. 6, 12 September

1926, only females were flying (in the evening); 13 September 1926, in the morning males and females were flying, one pair was *in coitu* and oviposition was going on; 23 July 1928, several spec.« (1929 was not mentioned).

The lakes described by Bartenev in such detail are easily identifiable as Khmelevskie Lakes, or Khmelevskiy Lakes, situated 3.3–5.7 km south-east of the Mount Achishkho summit (43.7235° N, 40.1326° E, 2 391 m a.s.l. on modern maps), on a short mountain range of the same name, and 4.2 km N – 5.7 km NNW of Krasnaya Polyana, a town in the Krasnodarskiy Kray of Russia. The lakes reside in the coordinate range of 43.71–43.73° N, 40.17–40.20° E at elevations from 1 703 to 1 875 m a.s.l. (Fig. 1) and have the status of the Ozera Khmelevskogo Nature Monument in the territory of Sochi National Park. This area is situated at the southern principal slope of the Great Caucasus Range and so formally refers to Asia. The common name for these lakes was proposed by the geographer and poet Yuriy Konstantinovich Efremov after a botanist, Vikentiy Ferdinandovich Khmelevskiy (1880–1933), who owned lands near the lakes, made their scientific description and studied flora and climate of that area in 1909–1914. Perhaps the lakes received their present name later than when Bartenev worked there. There are many lakes of different sizes, some hidden in the forest; their exact number is unclear and depends on the minimum size of a water body considered to be a lake. According to Valeriy Brinikh (pers. comm.), there are eleven lakes. Figure 1 shows best guesses as to which lakes Bartenev's ordinal numbers (except for No. 2) referred. The more remote lake inferred as Lake No. 6 has a specific name, Lake Zerkal'noe (Russ. 'Mirrory') and is not always considered belonging to the Khmelevskie lakes. Bartenev (1939) claimed Lake No. 1 and 2 to be as large as 300 m in diameter; currently the former is *ca* 50 m in diameter while the latter is *ca* 200 m long. However, the open depressions in which they lie are 250 and 300 m long, respectively, so a century ago the lakes could well have been larger.

Fate of type series

In the manuscript of her thesis, Belevich (2005: 51) mentioned among the specimens of *Aeshna juncea* (Linnaeus, 1758) she had studied the following: »The type material of *Ae.ju.atshichgo*: Achishkho, 10.09.1926 – 1♂; 10, 28.08.1927 – 2♂; 22.07.1928 – 4♀«. Only the last of these four dates was mentioned by Bartenef (1929a, 1930) – notably this was for the females. Howev-

er, other dates were close to those mentioned by Bartenev, so some confusion of hand-written dates by Bartenev himself, or by a technician, or by Belevich, cannot be excluded. Olga E. Belevich (pers. comm.) kindly communicated that she had studied those specimens in Zoological Institute of the Russian Academy of Sciences, Saint-Petersburg (ZISP) during the work on her thesis in 1999–2004. However, in spite of a thorough search, Andrey M. Medvedev upon his visit to ZISP in 2011 found neither these specimens nor any other of Bartenev's type specimens except for the holotype of *Trigomphus anormolobatus* Bartenev, 1912, and supposed wings of syntypes of *Denticnemis bicolor* Bartenev, 1956 (Medvedev *et al*. 2012). The author contacted those in charge of the ZISP insect collection (currently there is no special curator for Odonata) and they replied that the results of Medvedev's search are decisive and other Bartenev's types are unlikely to be found in that collection. The private collection of Bartenev is lost, but some syntypes might be found abroad if exchanged by Bartenev with foreign colleagues (Medvedev *et al*. 2012).

No syntypes of the taxa considered in this paper came to light and most probably they no longer exist. Therefore, this paper is based on topotypes, where available.

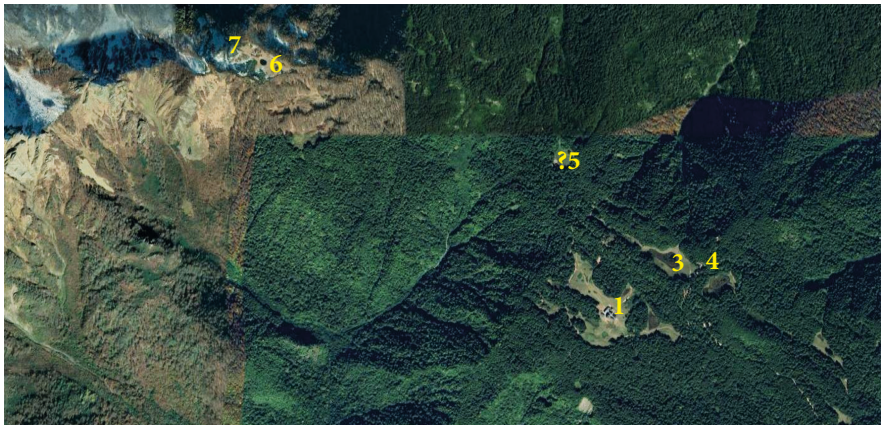

Figure 1. Aerial picture of the region *ca* 5 km north of Krasnaya Polyana, Krasnodar Krai, Russia, with the assumed situation of lakes No. 1–7 (except for No. 2) according to Bartenef (1930) among the Khmelevskie lakes south of the Mt Achishkho in the West Caucasus. Map data and picture: Google, ©2023 Airbus, CNES / Airbus, Maxar Technologies

Description of *Leucorrhinia circassica*

The description of *Leucorrhinia circassica* (Bartenef 1929a) was very detailed and contained about a thousand German words. The Russian version (Bartenef 1930) fully corresponded to the German original description, with some minor explanatory updates (see below). The description paid great attention to maculation of the body and wings, but structural characters are mentioned too. Variation among specimens of both sexes was also discussed. Unfortunately, this straight-forward description pays little attention to diagnostic characters and lacks a statement explaining why this series was considered a new species. Of other species, *Leucorrhinia dubia* Vander Linden, 1825, was mentioned five times (in two cases including *L. dubia orientalis* Selys, 1887, treated as a subspecies), and *L. pectoralis* (Charpentier, 1925) and *L. rubicunda* once. Ironically, all these allusions were made in the context of the new species' resemblance to rather than difference from those species! Only the following statements (given in English translation) can be considered as a kind of differential diagnosis:

»*Ia* [hamulus] almost straight and usually slightly lowered forward, more rarely vertical (as in *Leuc. dubia*). Apex of *Ia* narrowed but not acuminate, and directed upwards, not at all backwards (when the insect is viewed upside down). It is a characteristic of this species that *Ia* has a gently sloping, almost straight or somewhat concave posterior margin. This gently sloping posterior margin differs from the more vertical anterior margin of *Ia*. In rare specimens, the shape of *Ia* resembles *Leuc. dubia*.« (Bartenef 1929a: 56). The Russian version updates the last phrase with the following supplement: »(the forward inclination is less expressed and the posterior margin of *Ia* is not as gentle, by its situation less differing from the anterior margin of the latter)« (Bartenef 1930: 20).

»The genital plate of ♀ (Fig. 3) is similar to that of *Leuc. dubia*, but its posterior margin [surely the posterior margin of the lobes of the plate was implied] usually narrowed at middle but not pointed« (Bartenef 1929a: 57). The Russian version has the following appendix to this phrase: »less frequently completely similar to *Leuc. dubia*«.

The first description (Bartenef 1929a) and the subsequent paper (Bartenef 1929b) were illustrated with identical drawings (reproduced here in Fig. 1) of the dorsal view of tergites 6 and 7 in male (Fig. 1a), a lateral view

of the male secondary genitalia (Fig. 1b) and a ventral view of the female S8 and vulvar scale (Fig. 1c).

Description of *Enallagma cyathigerum* var. *rotundatum*

The description of *Enallagma cyathigerum* var. *rotundatum* (Bartenef 1929a) is short and worth providing in full in English translation: »Pale spots behind the eyes very large. The black band beneath these spots is 2 –> 2 times narrower than these spots. Appendices inferiores directed obliquely upwards; their apices higher than the lower surface of the appendices superiores. The inferior appendices do not posteriorly (seen in profile) reach (or reach but do not exceed) the middle of the length of the superior appendices. The superior appendices are longer on their upper side than on the lower side because the lower posterior part does not project backwards (as is the case of *Enall. cyathigerum cyathigerum*) (Fig. 11). The female of *atshischgho* does not differ from the f. typ. All specimens of *Enall. cyathigerum* originating from other localities of the Transcaucasus (Military Georgian Road, etc.) are typical *cyathigerum* nec *rotundatum*.«

Here we encounter two errors of the *lapsus calami* type. Firstly, for the female, the author used the Latin (in italics!) name *atshischgho* rather than *rotundatum* under which the taxon was described. In the same paper (Bartenef 1929a) the name *atshischgho* is given to a new subspecies of *Aeshna juncea* (Linnaeus, 1758), described from the same place. It seems that Bartenev initially was going to give the new variety of *E. cyathigerum* the same name, changed his mind later but forgot to rectify the text. Second, in the statement of the appendage relative length, the superior and inferior appendages (of which the latter are much longer) were confused.

The corresponding Russian (re)description in Bartenef (1930) is almost the same but is arranged in a table comparative to the typical *cyathigerum*. One more character is added: the projection of the lower-posterior (sic) margin of the upper appendages is directed inwardly, as seen from above, and so is not seen in profile. Curiously, the confusion of the superior and inferior appendages is retained. Beyond the table it was stated that the male from Lake No. 1 (22 July) was »less typical«, its lower appendages being almost horizontal. Also, the localities of *E. cyathigerum s. str.* in Transcaucasia were expanded as follows: Tiflis, the Kayshaurskoe Lake, the Bazaletskoe

Lake. Some male specimens from the latter were said to have less sharp but still noticeable [caudal] projection of the cerci and larger post-ocular spots, but still not approaching *rotundatum*.

Both the original description and subsequent papers were illustrated with the same drawing of the male appendages in lateral view (Fig. 1d).

Description of *Aeshna juncea atshischgho*

The description provided by Bartenef (1929a) is detailed and occupies 2.5 pages, including six drawings of the frontal and lateral views of the male thorax, of the lateral view of the female S2, the spines of the male S10, of the male genitalia and the female ovipositor. It lacks comparison with any other taxon, so leaving the issue of diagnostic characters completely obscure. This drawback was overcompensated in Bartenef (1929b), where *A. juncea atshischgho* was compared with five other subspecies of *A. juncea* (two new) in a table of 57 lines occupying, together with 32 figures, pages 37–49! This table was said to provide different »character states typical for each form«. However, when reading such original descriptions by Bartenev, one has to bear in mind that such tables are actually structured descriptions rather than indication of diagnostic characters: Bartenev just registered all differences noticed between series compared, including many overlapping quantitative ones. It is his free text that clarifies which characters he considered important and diagnostic and actually provides a differential diagnosis. Such text for the subspecies considered and another Caucasian subspecies, quite long and detailed as well, was provided on pages 50–52.

In brief, Bartenef (1929b) pointed out the fact that *A. juncea* in the Caucasus is present in rare scattered populations associated with certain highland lakes, which are far isolated from the main species' range. He had specimens from three localities in Georgia: females from Lake Kaishauri (42.438° N, 44.505° E, 1 780 m a.s.l.), a female from Gvileti Station (32 km N from the above, on the same Military Georgian Road), and a male from the 1st of Sakochavi Lakes (presumably 41.744 N, 43.461 E, 1 567 m a.s.l., 6 km W of Bakuriani). The specimens from Kaishauri and Sakchavi had been described by him as *Aeschna juncea* var. *crenatoides* (Bartenev 1925), »not defining its taxonomical value more precisely« (Bartenev 1925) and is treated in Bartenef (1929b) as a subspecies. This subspecies differs from

other subspecies of *A. juncea* by the very broad pale stripes of the thorax »deviating towards« those of *Aeshna crenata* Hagen, 1856, and by the vulvar scale »deviating towards the *A. clepsydra*-group«, with a very broad but shallow incision, so that its lateral lobes are not as expressed as in other subspecies of *A. juncea*. The males of *A. juncea atshischgho* deviate in the thorax pattern even more towards *A. crenata* than *A. juncea crenatoides*, of which Bartenev in 1929 had only one remaining male specimen, and have some minor differences in the pattern of the abdomen and the struc-

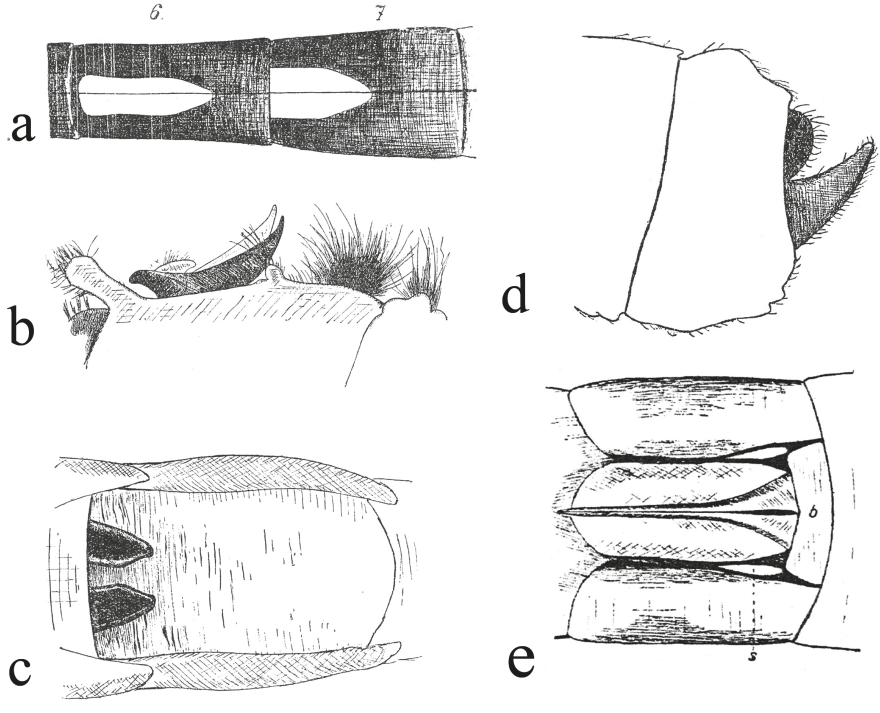

Figure 2. Drawings of details of *Leucorrhinia circassica* (a–c), '*Enallagma cyathigerum* var. *rotundatum*' (d) and '*Aeschna juncea* var. *atshischgho*' (e) reproduced from Bartenef (1929a: figs 1–3, 9, 11; 1929b: fig. 68; 1930: figs 1–3, 5, respectively): a – tergites 6 and 7 in dorsal view in male; b – male secondary genitalia in lateral view; c – S8 and vulvar lamina, ventral view; d – male appendages, lateral view; e – ovipositor, ventral view (Bartenev's designations therein: b – vulvar lamina, s – elongate lateral sclerites of S9 ('*lateral genital plates*' *sensu* Walker 1912). Not to scale.

ture of the secondary genitalia. The females of *A. juncea atshischgho* have the same coloration pattern as those of *A. juncea crenatoides* and even less expressed incision of the vulvar scale (Fig. 2e). So, *A. juncea atshischgho* is similar to *A. juncea crenatoides* but deviates even more in the same direction from typical *A. juncea*. However, the most striking feature of *A. juncea atshischgho*, differentiating it from *A. juncea crenatoides*, is the presence in females of 'lateral genital plates' *sensu* Walker (1912), which are paired lateral sclerites of the S9 sternite looking like anteriolateral folds in the proximal part of the space between the vulvar lamina, S9 tergite margin and genital valves v3. These 'lateral genital plates' are normally absent in species of the *A. juncea* group but present in other species groups of the genus. In *A. juncea atshischgho* they vary from short to narrow and long, the latter state is shown in a drawing (Bartenef 1929a: fig 9; Bartenef 1929b: fig 68; reproduced in Fig. 2e in this paper).

Material and methods

The Kmelevskie Lakes, the type locality of the three taxa considered, were inspected by the author on 10.vii.2008, a day partly sunny and partly rainy. Lakes with presumed Bartenev's numbers 3, 4, 6 and 7 were visited. The lakes were situated in depressions of the Achishkho Range section with a rather flat but uneven surface covered with thick beech (*Fagus orientalis* Lipsky) forest.

The presumed lake No. 3 (Fig. 3) (43.717–43.718° N, 40.200–40.20° E, *ca* 1 761 m a.s.l.) was 185 × 80 m and teardrop-like in shape. It lay in a depression twice as large, the slopes of which were covered with lush subalpine meadow, with a large house at its eastern margin. The banks were bordered with a strip of sedge, mostly *Carex rostrata* Stokes, then followed a narrow open water zone, where the depth sharply increased up to *ca* 1.3 m, and then a floating bog formed by *C. rostrata* and *Sphagnum* sp., strong enough to walk on, which occupied most of the lake area, leaving open water, deep blue-green in colour, in several large, irregular 'windows' (Fig. 3).

The presumed lake No. 4 (43.716–43.717° N, 40.204–40.205° E, *ca* 1 765 m a.s.l.) was 111 × 60 m, oval in shape, had a narrower surrounding meadow and was almost completely covered with thick floating matted vegetation leaving just few open 'windows' and a narrow open margin along the banks.

The presumed lake No. 6 (43.727–43.728° N, 40.173° E, *ca* 1 875 m a.s.l.); 38 × 34 m, oval in shape, was situated in a shallow depression on a bare ridge top covered with meadow and used for cattle grazing. It had clear water and grassy banks with just few patches of sparse *C. rostrata* and without any *Sphagnum*.

The presumed lake No. 7 (43.728° N, 40.172° E, *ca* 1 877 m a.s.l.); 44 × 42 m, subtriangular in shape, situated in a depression neighbouring the previous one. Unlike the previous lake, it was almost entirely covered with a sedge/peat moss floating rafts leaving just two 'windows' of open water 2–3 m in size.

In the water at sedge/peat moss floating rafts of lakes No. 3 and 7, numerous larvae of Libellulidae and Aeshnidae (*cf. A. juncea*) of different stages were found. Among the sedges at the banks of the non-mossy lake No. 6, numerous large aeshnid larvae were found but no Libellulidae.

Two immature male topotypes of *L. circassica* were collected in the vegetation near lake No. 3, one on a beech leaf (Fig. 4a) and one on a leaf of *Veratrum lobelianum* Bernh. (Figs 4b, c). Their wings were still glittering weakly, and all pale body markings were still yellow. Four teneral topotype females of that species were collected, plus several teneral individuals observed, by N. Priydak at lake No. 4. Besides, three imagines of *Libellula quadrimaculata* Linnaeus, 1758) were encountered at lake No. 3. Neither adults nor larvae of Zygoptera were found.

In 2013, the Khmelevskie lakes were visited by Andrey F. Medvedev. He also collected some topotypes of *L. circassica* (not studied here) and a single topotypic male of *Enallagma rotundatum*, which he kindly offered (in 96 % alcohol) for this study. Its label is as follows: West Caucasus, at Mt Achishkho, Lake Zerkal'noe (the former Achishkho Meteorological Station) [presumedly Bartenev's lake No. 6], 1 888 m a.s.l., 25.vii.2013, leg. A. Medvedev.

Additional material used for comparison, listed under the names used by the providers of specimens:

Enallagma cyathigerum risi Schmidt, 1961

20♂♂ — Tadjikistan, Kulyab Province, Lake Sharak (Chil' Dukhtaron) 6 km NW of Chil' Dukhtaron village, 38.2808° N, 70,0392° N, 1 670 m a.s.l., 21.vii.1987, leg. S.N. Borisov.

Figure 3. The presumed lake No. 3 from Bartenef (1930) of the Khmelevskie lakes, Krasnodarskiy Krai, Russia. Type locality of *Leucorrhinia circassica*, *Enallagma cyathigerum* var. *rotundatum* and *Aeschna juncea* var. *atshischgho*. Photos: OEK (10.vi.2008)

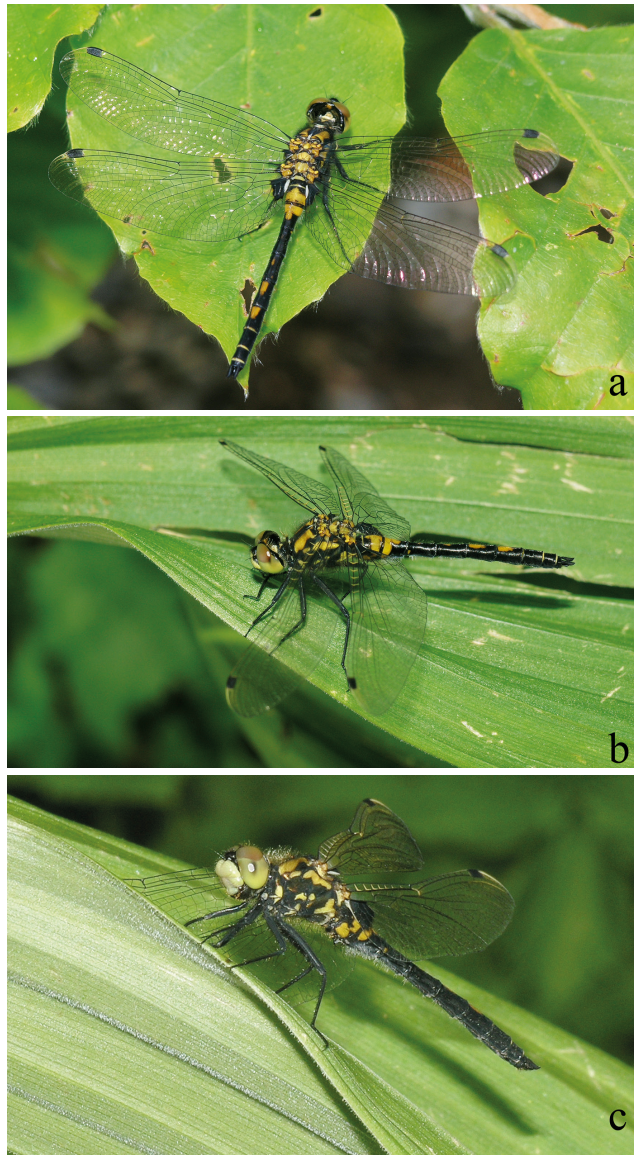

Figure 4. Two (a–b and c) subteneral male topotypes of *Leucorrhinia circassica* photographed in nature in their type locality at the Khmelevskie Lakes, Krasnodarskiy Krai, Russia, presumed lake No. 3 by Bartenef (1930). Photos: OEK (10. vi.2008)

Enallagma deserti (Selys, 1871)
13♂♂ — Morocco, Middle Atlas, Aguelmam Afennourir, 18 km SSW of Azrou, 33,2786° N, 5.2522° W, 1 815 m a.s.l., 21.vii.2010, leg. Jean-Pierre Boudot.
Aeshna juncea (Linnaeus, 1758)
1 teneral ♀ — Russia, W Caucasus, Republic of Adygea, Lagonaki Plateau, a small round permanent pool amidst subalpine meadows at the north-eastern foot of Mt Oshten, 44.0184° N, 39.9707° E, 2 048 m a.s.l., 12.vii.2008, leg. O. Kosterin; 1 ♀ — Russia, central N Caucasus, Karachay-Cherkes Republic, Zelenchuk District, 7 km SW of Nizhniy Arkhyz, Lake Taza-Kel' (Forelevoe) at the Bol'shoy Zelenchuk River left bank, 43.6343° N, 41.3923° E, 1 261 m a.s.l., 3.vii.2019, leg. V. Onishko et O. Kosterin; 4 teneral ♀♀ — Russia, E Caucasus, Republic of Dagestan, Agul District, Lake Chirag near Chirag village, 41.800 N, 47.408 E, 2 015 m a.s.l., 18.vii.2021, leg. E.V. Ilyina.

In this paper, references 'Fig.' are capitalised when referring to illustrations in this paper and are all lower case, 'fig.', when referring to figure numbers in the cited literature sources.

Taxonomic status of *Leucorrhinia circassica* Bartenef, 1929

From the contemporary point of view, in the case of *L. circassica* Bartenev had not sufficient reason to propose a new species, which could be, and *de facto* has been, synonymised with *L. dubia* without further investigation. Most of the original description (Bartenef 1929a) evinces, both implicitly and explicitly, that *L. circassica* corresponds to *L. dubia* in all its coloration characters more to *L. dubia dubia* than to *L. dubia orientalis*, although resembling the latter with respect to the underdevelopment of pale spots on tergites 4 and 5 (Bartenef 1929a, 1930). The only difference of *L. circassica* from *L. dubia* was considered to be the unusually 'rectified' shape of the hamulus in some (!) male specimens and narrowing lobes of the vulvar scale in some (!) female specimens among the type series. To strengthen the impression of a different taxon, Bartenev illustrated the versions of these structures most deviating from the *dubia*-type. However, the claimed high intra-population variation in the structure of even important reproductive organs, ranging from the typical state for *L. dubia* to some deviated state,

by no means can be considered evidence of this population to comprise a different species. It just illustrates the potential of intra-species variability in *L. dubia*.

The general habitus of both male topotypes of *L. circassica* is presented in Figure 4; their secondary genitalia in Figures 5a–b; the female topotype vulvar lamina in Figure 5c. In the topotypes examined, the hamulus shape has nothing in common to that described verbally and depicted by Bartenef (1929a; 1930; see Fig. 2a) but has a structure typical of *L. dubia*: both its hooks are bent so that their apices are directed nearly perpendicular to the body; compare to figures in Dijkstra *et al.* (2021: 275, figs). The vulvar lamina of the female paratype (Fig. 5c) is also of the structure typical for *L. dubia* (*cf*. Dijkstra *et al.* 2021: 275).

In view of the above the following synonymy is proposed:
***Leucorrhinia dubia* (Vander Linden, 1825), valid name**
syn. *Leucorrhinia circassica* Bartenef, 1929

I do not use the formula 'syn. n.', which is not regulated by ICZN (1999), since this synonymy was repeatedly supposed in many literature sources (*e.g.*, Kalkman *et al.* 1994, 2015; Skvortsov 2010; Onishko & Kosterin 2021) and is implemented in recent summarising works (*e.g.*, Boudot & Kalkman 2015; Malikova & Kosterin 2019; Onishko & Kosterin 2021), which do not recognise *circassica* as a valid taxon of any rank.

The nature of the anomalous hamulus shape, depicted with both hooks 'unbent' (Fig. 2a), in some (most probably no longer existing) male syntypes by Bartenef (1929a, 1930; see Fig. 2a) is unclear.

Taxonomic status of *Enallagma cyathigerum* var. *rotundatum* and reconsideration of the Palaearctic *Enallagma* spp. with the *boreale*-type male cercus

After publications by Bartenev (1929a, 1930), the name *E. cyathigerum rotundatum* was applied to specimens other than Bartenev's type series only by two authors. St. Quentin (1964) identified under this name one female and two male specimens originating from two sites situated to the north and

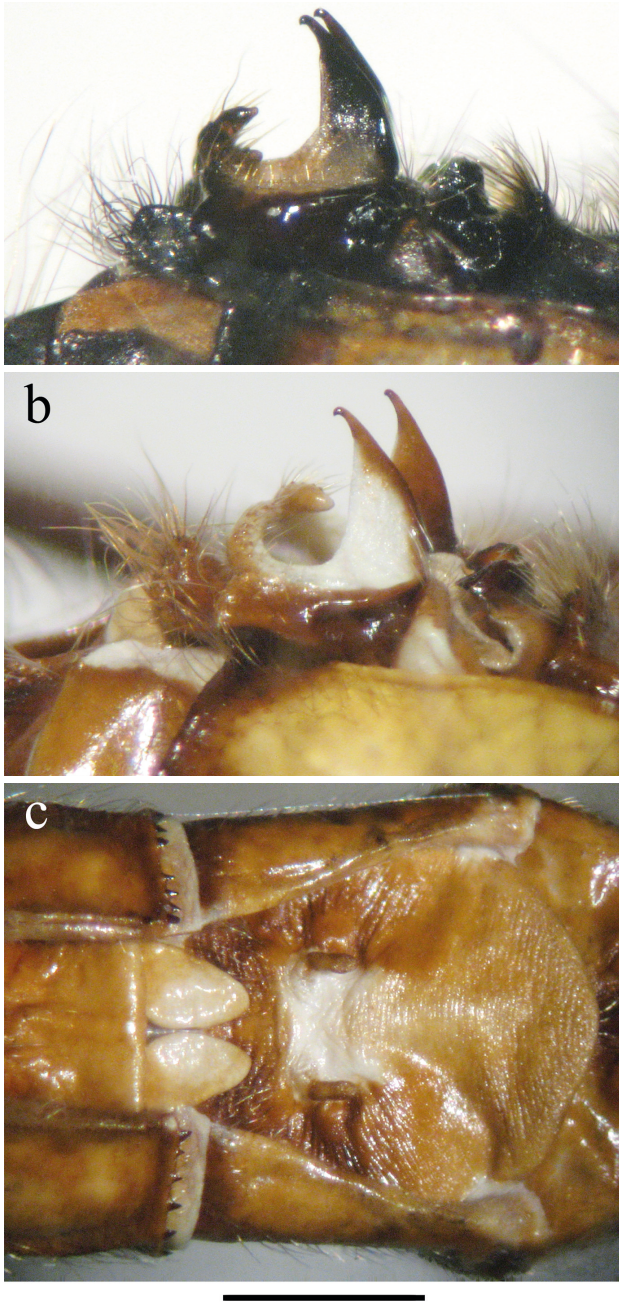

Figure 5. Structures of two different male topotypes and the female topotype of *Leucorrhinia circassica*. Khmelevskie Lakes, Krasnodarskiy Krai, Russia, presumed lake No. 3 from BARTENEF (1930), 10.vi.2008: a – male secondary genitalia, lateral view; b – ditto, latero-posterior view; c – female S8–9, ventral view. Scale bar 0.5 mm.

south of Sultan-Dag in central Anatolia, Akşehir and Budur-Göl. He based this on the 'ventral branch' of the male cercus not or scarcely seen in lateral view. In a subsequent paper devoted to the Odonata fauna of Anatolia and adjacent regions, which did not concern geographical data (St. Quentin 1965), he listed both typical *E. cyathigerum* and *E. cyathigerum rotundatum*, the latter obviously based on specimens reported in his previous paper. St. Quentin (1965b) also followed Schmidt (1961) and supposed that the taxa *deserti* and *rotundatum* might be synonyms. Later, Demirsoy (1982) attributed all *E. cyathigerum* from Turkey to *E. cyathigerum rotundatum*, without any taxonomic comment and probably based on St. Quentin (1964, 1965b). This was obviously a misidentification since his own drawings (Demirsoy 1982: fig. 44) show the appendages of *E. cyathigerum s. str.*, which is known to occupy Turkey (Boudot *et al.* 2021).

Among authors who published since 1973, Jurzitza (1975) mentioned the name *E. c. rotundatum* as valid with respect to Bartenev's work. Hence, at least two authors, Jurzitza (1975) and Demirsoy (1982), used this name as valid less than 50 years ago. Therefore, it cannot be rejected as *nomen oblitum* under the provisions of Article 23.9 of International Code of Zoological Nomenclature (ICZN 1999).

In the original description of *E. cyathigerum rotundatum*, four characters were mentioned concerning: (i) the extent of the pale and black colours on the head, (ii) the direction of the cercus, (iii) the relative lengths of appendages and (iv) the cercus structure. The colour character is rather irrelevant in view of the well-known enormous intra-species variation of *Enallagma cyathigerum* in this respect (*e.g.*, Dijkstra *et al.* 2021), while the morphological characters deserve attention.

The anal appendages of the topotype male of *E. cyathigerum rotundatum* are shown in Figure 6a. They do not exhibit Bartenev's characters (ii) and (iii): the paraproct is directed much more backward than up, as usual in *E. cyathigerum*, and all appendages are of the length normal for *E. cyathigerum*. Importantly, the cercus is not as short as shown by Bartenef (1929a, 1930) (Fig. 2c). The paraproct direction could be an unstable character, as Bartenef (1930) himself stated that in the male from lake No. 1 they are »almost horizontal«. I used to examine numerous males of *E cyathigerum*

and found the paraproct direction rather stable and similar to the topotype considered. At the same time, I found it variable among specimens in the examined series of *E. deserti* from Morocco (Figs 6c–e), where, *e.g.*, a specimen shown in Fig. 6c has the paraprocts slanting up almost as in Bartenev's drawing of *rotundatum* (Fig. 2c).

One explanation of the unusually short cerci, as well as to some extent of the paraprocts, in the drawing and description of *E. cyathigerum rotundatum*, pointed out also by Lieftinck (1966), could be that Bartenev probably made his drawing from not perfectly lateral but somewhat anterio-lateral view, and then made his description based on the drawing. Another explanation could be that he again took a slightly aberrant specimen for description.

At the same time, in lateral view, the cercus of the topotype is rounded (Fig. 6a, left) exactly as shown by Bartenev (Fig. 2c), with a minor difference in the presence of a small basoventral tubercle. However, Bartenef (1930) specially pointed out that this tubercle was present but not seen in the illustrated side view. Perhaps it was hidden by the S10 hind margin in his drawing if the above supposition of imperfectly lateral angle is correct. This projection is a yellow lobe positioned on the cercus below and proximally of the robust black terminal tooth. This lobe is scarcely seen in lateral view (Fig. 6, left column), visible in dorsal view (Fig. 6, middle column) but best seen in oblique inner dorsolateral view (Fig. 6, right column; there the lobe is indicated with a green asterisk). Bartenev obviously considered the cercus shape most important, as it is reflected in the name *rotundatum*. The concordance of the cercus shape between the type series and the examined topotype suggests that during the 80 years between his last and my expeditions to the type locality it was inhabited by the same population, which the topotype represents well.

The cercus structure illustrated by Bartenef (1929a; 1930) and observed in the topotype of *E. cyathigerum rotundatum* represents the so-called (Stoks *et al.* 2005) *boreale*-type cercus. It has a rounded profile, without a terminal projection as in *E. cyathigerum cyathigerum* but with a subventral lobe or tubercle (often referred to as 'lip') occupying a ventral position proximal of the robust, sclerotised terminal tooth (Fig. 6, right row, indicated with

the green asterisk). This cercus type is known to be shared by the following taxa:

- *Enallagma deserti* from North Africa. The original combination was *Agrion deserti*; the type locality is »Algeria, Lamb. Eth.«, probably Lambessa (Selys 1871);
- *Enallagma risi* or, alternatively, *E. cyathigerum risi*, which broadly ranges from East Europe, Central Asia, and eastern South Siberia to the Middle Amur River basin (Onishko & Kosterin 2021). Its type locality is »Achmede Dewane« in Nuristan, Afghanistan (Schmidt 1961). This taxon has two junior subjective synonyms (Dumont 1975; May 1977): *E. strouhali* St. Quentin, 1962, with type locality: China, Harbin (St. Quentin 1962), and *E. cyathigerum mongolicum* Benedek, 1968, with type locality: Mongolia, Chovd Aimak, 30 km SE of Chovd, SW bank of Char Us Nuur (Benedek 1968). This taxon also has a junior homonym, *Enallagma risi* Pinhey, 1962, with the current valid name *Pinheyagrion angolicum* (Pinhey, 1966) (Pinhey 1966; May 2002).
- *Enallagma circulatum* Selys, 1883, from Japan, the Kurile Islands and southern Sakhalin; the type locality was mentioned as »Japon« (Selys 1883). This taxon has three junior subjective synonyms, *Ischnura karafutonis* Matsumura, 1931 (syntypes from several localities in Sakhalin), *E. deserti jezoensis* Asahina, 1949 (type locality: Hokkaido, Kuttyaro-ko) and *E. belyshevi* Haritonov in Belyshev et Haritonov, 1975 (type locality: Iturup Island, Kuybyshevka) (Asahina 1989; Paulson *et al*. 1998).
- *Enallagma boreale* (Selys, 1875), the Nearctic species (Ris 1928; Schmidt 1961; Dumont 1975; Seidenbusch 1997; Stoks *et al.* 2005).

For good illustrations of the *boreale*-cercus structure in *E. deserti* see Ris (1928: fig. 1), Lieftinck (1966: fig. 5) and Jurzitza (1975: fig. 7), and in the taxon known as *E. risi* or *E. cyathigerum risi* see St. Quentin (1962: figs 1, 2 sub *E. strouhali*), Benedek (1968: figs 3, 5, sub *E. cyathigerum mongolicum*), Dumont (1975: figs 1–3), May (1997: figs 6A–E), Seidenbusch (1999: fig. 5; sub *E. risi*), Kosterin (2004: fig. 5; sub *E. cyathigerum risi*), Stoks *et al.* (2005: fig. 1), Kosterin & Zaika (2010: fig 4c; sub *E. cyathigerum risi*), Kosterin & Ahmadi (2018: fig. 33a; sub *E. cyathigerum risi*). In the original description of *E. risi*, the profile of the cerci is well illustrated (Schmidt

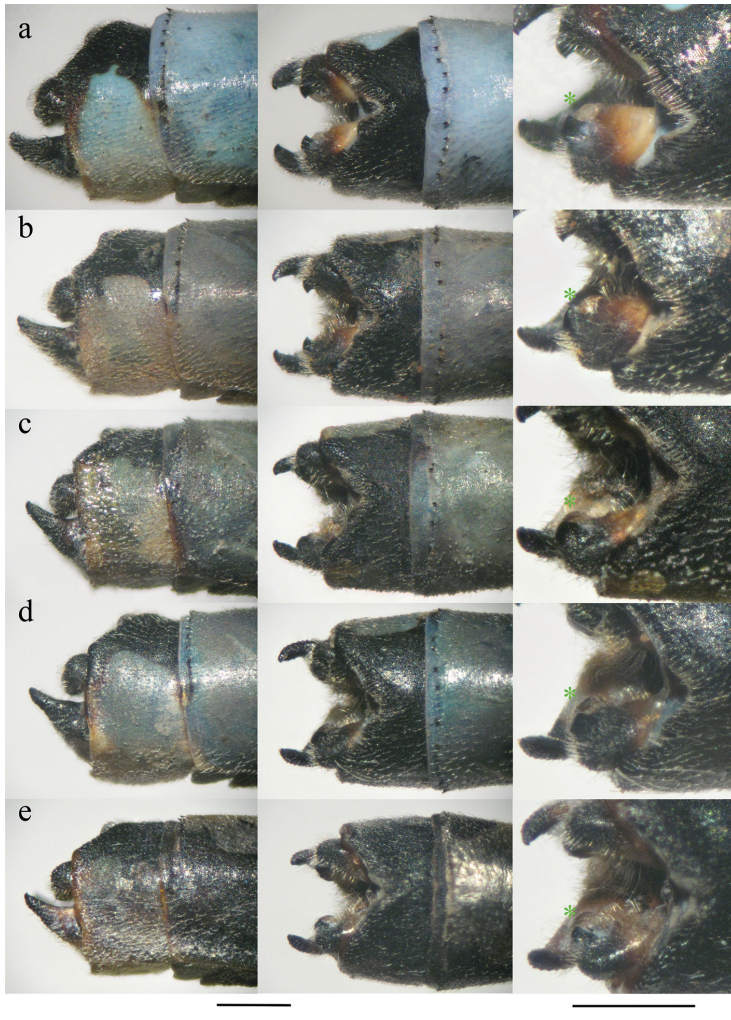

Figure 6. Male anal appendages (left – lateral view; centre – dorsal view; right – cercus, oblique dorsolateral view) of *Enallagma* spp. (taxonomic treatment as provided): a –Topotype of *E. cyathigerum* var. *rotundatum* Bartenef, 1929, West Caucasus, at Mt Achishkho, Lake Zerkal'noe, 25.vii.2013, A. Medvedev leg.; b – *Enallagma cyathigerum risi* Schmidt, 1961, Tajikistan, Kulyab Province, Lake Sharak (Chil' Dukhtaron), 21.vii.1987, S.N. Borisov leg.; c–e – *Enallagma deserti* Schmidt, 1961, Morocco, Middle Atlas, Aguelmam Afennourir, 18 km south-west of Azrou, 21.vii.2010, J.-P. Boudot leg. The subventral lobe ('lip') of the cercus is indicated with green asterisks. Scale bar 0.5 mm.

1961: fig. 2c, d) while the dorsal view (fig. 2b) shows an unnatural structure as if formed by merged subventral lobes of both cerci, perhaps contaminated by faeces in the specimen depicted. Belyshev (1973: fig. 251g, m) also showed the same cerci profile (sub. *E. cyathigerum*) but the lip is not resolved because of the small size of the figure. Schneider *et al.* (2018: fig. 11c; sub *E. cyathigerum risi*) illustrated the appendages but for some reason did not show the yellow subventral lobe. The similarity of *E. boreale*, *E. deserti*, *E. circulatum* and *E. risi* in overall larval and adult morphology has been acknowledged by Westfall & May (1996), while Stoks *et al.* (2005) evaluated very close similarity in their cercus structure by means of quantitative morphometry.

This *boreale*-type cercus structure differs from the *cyathigerum*-type one, according to Stoks *et al.* (2005), found in the Palaearctic *E. cyathigerum s. str.* and the Nearctic *E. annexum* (Hagen, 1861) and *E. vernale* Gloyd, 1893. In the *cyathigerum*-type cercus, the yellow lobe prolongs toward and under the terminal tooth, which is narrower and lest robust, and protrudes caudad of it (Westfall & May 1996; Stoks *et al.* 2005), as illustrated for *E. cyathigerum* by Ris (1928: fig. 2), Lieftinck (1966: figs 4a–c), Jurzitza (1975: fig. 2), Demirsoy (1982: fig. 44b, sub *E cyathigerum rotundatum*), Stoks *et al.* (2005: fig. 1); Kosterin & Zaika (2010: fig. 4a); and Dijkstra *et al.* (2020: 119).

Actually, the proximal part of this yellow lobe may be also seen from above proximal to the tooth in *E. cyathigerum*, as depicted by Benedek (1968: fig. 6 »European specimens«) and Schneider *et al.* (2018: fig. 11d, Iran, Mazandran, Lake Valasht). According to my experience, in *E. cyathigerum cyathigerum* from the taiga zone of the Asian part of Russia, namely in Siberia in Tomsk Province, Todzha Depression in Tuva, in south Yakutia and Kamchatka, but also from Dagestan, this lobe is not seen at all from above; this version can be called 'the hyper-*cyathigerum*-type'. So earlier I interpreted some specimens from Middle Ural, Altai, and Tuva, where it was seen from above, as 'intermediate between *cyathigerum* and *risi*' and illustrated their cerci in Kosterin & Zaika (2010: fig. 4b) and Kosterin & Ahmadi (2018: fig. 33b). Such 'intermediate' males were recently reported from Georgia (Schröter *et al.* 2015) and even from Moscow (Onishko 2022) and may actually be the typical European version of *E. c. cyathigerum* (see Benedek

1968: fig. 6). It appears that the distribution and taxonomic value of the character of visibility of the yellow lobe in dorsal view in the *cyathigerum*-type cerci deserves thorough investigation. Anyway, in the *boreale*-type cerci the entire lobe is situated proximal to the terminal tooth and never protrudes caudad of it, while in the *cyathigerum*-type it always protrudes caudad as 'a nose', providing a simple character to distinguish these types.

Bartenef (1929a, 1930) considered his *E. cyathigerum* var. *rotundatum* close to *E. deserti*. The latter taxon was originally based on colour characters (Selys 1871). Ris (1929) provided a detailed redescription of this 'forgotten damselfly' basing on one male specimen from Saida, Oran Province, Algeria, which he compared with a long series of *E. cyathigerum* and also with some American species. Most of his description concerns the black pattern of the body and hardly deserves attention in view of its great variability in the Palaearctic *Enallagma* spp., namely *E. cyathigerum* and *E. circulatum*. The pale venation could have some importance. Of great importance is the precise description and illustration of the specific structure of the male cercus of *E. deserti* (Ris 1928: fig. 1) and its comparison with that of *E. cyathigerum* (Ris 1928: fig. 2). Lieftinck (1966) reconsidered what he called the '*E. deserti* problem', with respect to the holotype of *E. deserti* from Tunisia he examined, the description by Ris (1928) of the male from Algeria, and his own specimens from submontane areas of Morocco. He found out that both Tunisian specimens had strongly reduced dark patterns and that the pale venation of the holotype could be due to prior preservation in some liquid, while his Moroccan specimens of *deserti* did not differ from the European *E. cyathigerum* in any respect but the difference in the male cercus which he illustrated but considered to be 'slight'.

Ris (1928) also acknowledged that male specimens from 'Turkestan' have the cerci similar to *E. deserti* but did not attribute those specimens to that species. In fact, Schmidt (1961) just proposed the name *Enallagma risi* for the Central Asian taxon which was recognised from 'Turkestan' by Ris (1928) as having characteristic male cerci resembling those of *E. deserti* but left unnamed. Schmidt (1961: 409) just cited Ris's description instead of providing his own, but since Ris's description was referenced (and even cited) in the text, this conforms to the ICZN Art. 13.1. This citation concerned

only the cercus structure, which only is actually important, as follows: »On the other hand, the Turkestan specimens, which agree among themselves, show the dorsal branch with the apex medialward much like in the Central European ones, but the ventral branch (Fig. 2b) is shorter ... than the dorsal one, is covered by this in a pure dorsal view and accordingly does not appear in the side view as a ventral–distal process: the side view is thus very similar with that of *E . deserti*« (Ris 1928: 280; translated from German).

Schmidt (1961) specially indicated four males and one female from the type locality in Afghanistan as »Typen«, that is, as a series of syntypes and provided measurements for them. However, he considered specimens from Kashghar, Kashmir, and Central Mongolia belonging to the same taxon, although he did not include them in the type series.

Strikingly, in the same work where *E. risi* was described, Schmidt (1961: 410; translated from German) reported *E. deserti* for Iran: »In this context it may be of interest that 1♂ from Marus-Bar, 100 km WNW Meshed, Iran (coll. m.) belongs to *E. deserti*, and even the costal half of the wing except for the radius has light wing veins like in North African ♂♂ of *E. deserti*!«. Currently, such specimens from Iran are attributed to *E. risi* (Kosterin & Ahmadi 2018; Schneider *et al.* 2018). Most importantly, neither Ris (1928) nor Schmidt (1961) explicitly reported any difference between the Central Asian specimens (including the type series of *E. risi*) and *E. deserti*! Based on Schmidt's note about the pale venation of the Meshed male it can be supposed that he recognised the difference in the venation colour and so described a new species instead of identifying his Afghan series as *E. deserti*, as he did for his Iranian male.

Schmidt (1961) was informed about the existence of *E. cyathigerum* var. *rotundatum* but, like Bartenef (1929a), associated it with *E. deserti* rather than with *E. risi*: »*Enallagma cyathigerum* var. *rotundatum* Bartenef 1929d, p. 63f., fig. 11 from the W Caucasus could also belong to *E. deserti*, as neither the description nor the image of the app. sup. contradicts that!« (Schmidt 1961: 410; translated from German).

These considerations revive the issue of relationship between the taxa *deserti*, *rotundatum* and *risi*. In spite of the similarity of the *boreale*-type cercus structure across the taxa that have it (Stoks *et al.* 2005), from the above cited illustrations one can see that this structure is not identical in all of them. In

particular, in *E. circulatum* the rounded posteriolateral 'head' of the cercus is enlarged and swollen as compared to other species of the group (Jurzitza 1975: fig. 8, sub *E. deserti circulatum*; Seidenbusch 1997). In *E. deserti*, the yellow ventral lobe is large, disposed immediately under the robust terminal black tooth, as shown for a specimen from Algeria by Ris (1929: fig. 1; no fold is shown), specimens from Morocco by Lieftinck (1966: fig. 5) and Jurzitza (1975: fig. 7) and here in Figs 6d–e. In the Moroccan specimens examined by me and illustrated by Lieftinck (1966), the ventral lobe has a fold parallel to its margin which give it the appearance of two superimposed sea waves (Figs 6d–e; Lieftinck 1966: fig. 5). At the same time in the taxon *risi*, this lobe is smaller, has no fold, and is shifted proximally from the robust terminal tooth and is clearly separated from it, as specially pointed out by Benedek (1968) and illustrated in Fig. 6b and earlier, under the name *risi* or its synonyms, by many authors referenced above.

It was repeatedly supposed, solely on the base of the cercus structure illustrated by Bartenef (1929a; 1930; Fig. 2c), that *E. cyathigerum* var. *rotundatum* Bartenef, 1929 is a senior subjective synonym of *E. risi* Schmidt, 1961 (Kosterin 2004; Kosterin & Zaika 2010; 2011; Schröter *et al.* 2015; Onishko & Kosterin 2021; Boudot *et al.* 2021). The taxon *risi* used to be regarded to occupy open, semiarid to arid territories from the Volga River in the west to East Siberia and Mongolia in the east and Iran and Afghanistan in the south, and being replaced by *E. cyathigerum s. str.* in Western and Central Europe, Asia Minor and the forest zone of Asia. In particular, the latter is common in the taiga zone, from Scandinavia to Kamchatka, especially in peat moss habitats (Kosterin 2004; Dumont *et al.* 2005; Kosterin & Zaika 2010, 2011; Onishko & Kosterin 2021). Clear ecological segregation of these two taxa was observed in Tomsk Province (Bernard & Kosterin 2010) and Tuva (Kosterin & Zaika 2010, 2011), despite existence of populations with intermediate characters in the latter region. From this point of view until recently it looked unnatural for the taxon *risi* to inhabit peat-moss lakes surrounded by beech forest in moist and cool highlands of the West Caucasus, such as the type locality of *E. cyathigerum* var. *rotundatum* (Schröter *et al.* 2015). Therefore, before the topotype of the latter was analysed, it would be reasonable to suggest that its type series, or just the holotype, were represented by somewhat ab-

errant specimen(s). In this respect the note by Bartenef (1929a) looked important that he had obtained the typical *E. cyathigerum* from Transcaucasia, 'Militär-Georgische Straße'. This means the road Vladikavkaz-Tbilisi, and the localities were expanded by Bartenef (1930) as Tiflis and Lakes Kaishur and Basaleti.

However, still unpublished data of 2019–2021 by Vladimir Onishko and myself suggest that such ecological segregation does not take place in the Russian Far East and the Caucasus. A population identifiable as *risi* was found in 2020 on a pond in Korfovskiy Settlement in the southern Khabarovskiy Kray (Onishko & Kosterin 2021), in the zone of humid mixed forests of the Manchurian type. Our joint expedition of 2019 to the Caucasus within Krasnodarskiy Kray and Karachay-Cherkes Republic, occupying the central North Caucasus west of Mt Elbrus, invariably revealed only specimens identifiable as *risi*, with no 'intermediates' found among 29 male specimens collected at seven localities situated from seal level to 1 700 m a.s.l. at the quite humid headwaters of the Zelenchuk River. So, it became clear that the West Caucasus is occupied throughout by the taxon identifiable as *risi* and Bartenev's finding represented no anomaly. The distribution of *risi* is obviously contiguous from West Caucasus to the southern Russian Plain, occupied with the same taxon, *e.g.*, at Elista (OEK unpubl.) and Samara (Kosterin 2004), and then to Kazakhstan and Central Asia.

At the same time, our expedition of 2021 to Dagestan, East Caucasus, revealed only *E. cyathigerum s. str.* – 16 male specimens from six localities situated from 180 (semiarid foothills) to 2 400 m a.s.l. This is in line with occurrence of this taxon in Georgia (Bartenef 1929a, 1930; Schröter *et al.* 2015). It may be that all or most of the East Caucasus, probably east of the Mt Elbrus, is occupied by *E. cyathigerum s. str.*

According to my experience (Kosterin 2004; Kosterin & Zaika 2010; Kosterin & Ahmadi 2018; Onishko & Kosterin 2021; and unpubl. observations), the cercus structure in specimens identifiable as *risi* is very stable across their vast range outlined above. Among specimen series available to me, for comparison with the topotype of *E. cyathigerum* var. *rotundatum* I chose the one from Kulyab Province of Tajikistan, collected closest (*ca* 300 km NNW) to the type locality of *risi* in the Nuristan Province of Afghanistan. It included 20 males that were fairly homogeneous as to

their structural characters and quite similar to *risi* from elsewhere. The anal appendages of one of these specimens shown in Figure 6b, including the cercus, are nearly identical to those of the topotype of *E. cyathigerum* var. *rotundatum* (Fig. 6a), hence fully confirming identity of the taxa *rotundatum* and *risi*.

Based on the above considerations, the following taxonomical statement concerning the nominal taxa, in their original combinations, is put forward:

***Enallagma cyathigerum* var. *rotundatum* Bartenef, 1929**
Enallagma risi Schmidt, 1961, syn. nov.
Enallagma strouhali St. Quentin, 1962, syn. nov.
Enallagma cyathigerum mongolicum Benedek, 1968, syn. nov.

Benedek (1968, sub *E. cyathigerum mongolicum*), Dumont (1975), May (1997) and Seidenbusch (1997; 1999) stated that the female mesostigmal plate in *risi* has its anterior ridge more strongly raised than in *cyathigerum s. str.*, obviously to fit the different structure of the male cerci. Unfortunately, we do not have female topotypes of *E. rotundatum*. The characters of the male topotype of *E. cyathigerum* var. *rotundatum* other than the cercus structure correspond to both *risi* and *cyathigerum s. str.*, which do not differ in anything else, but the latter exhibits a much greater variation of the black pattern extent.

The proper taxonomic rank of *rotundatum* is another issue. Its junior synonym, *E. risi*, was considered a *bona fide species* by several authors (Stoks *et al.* 2005; Turgeon *et al.* 2005; Bernard & Kosterin 2010; Callahan & McPeek 2016; Boudot *et al.* 2021), while others regarded it as the subspecies *E. cyathigerum risi* (Samraoui *et al.* 2002; Kosterin & Zaika 2010, 2011; Schröter *et al.* 2015; Kosterin & Ahmadi 2018; Schneider *et al.* 2018). Authors from both parties used molecular phylogeny in their attempts to clarify the issue (Samraoui *et al.* 2002; Turgeon *et al.* 2005; Callahan & McPeek 2016). It is crucial that in Middle Ural (Sverdlovsk Province), Altai Mts (Kosterin 2004), and Tuva (Kosterin & Zaika 2010, 2011), transition populations exist with males having both *boreale*- and *cyathigerum*-types of the cerci, while the *cyathigerum*-type is represented

by the subtypes with the yellow lobe either visible or concealed in dorsal view. Also, in the Shilanehar valley, Markazi Ostan and Central Iran, a specimen with the *cyathigerum*-type cerci was found among specimens with the *risi*-type cerci (Kosterin & Ahmadi 2018). That intra-population variation with respect to the position of the yellow lobe, and also absence of any other reliable differences between the two taxa in question, made me to consider the taxon known as *risi* a subspecies *E. cyathigerum risi* (Kosterin 2004; Kosterin & Zaika 2010, 2011; Onishko & Kosterin 2021). Those transition populations seem to occur between the areas occupied by pure structural types, a pattern typical for subspecies, while occasional hybrids between good species would be found in broad areas of their co-occurrence, which is not the case.

The phylogenetic reconstruction based on AFLP analysis of nuclear DNA by Turgeon *et al.* (2005) showed that *E. risi* (the name used in this publication) was nested inside the paraphyletic *E. cyathigerum* [*s. str.*] clade. Haplotypes of the 842-bp long fragment of mitochondrial DNA from the *COI* to *COII* genes of the Palaearctic *Enallagma* spp. analysed by the same authors were highly monophyletic as a whole. *Enallagma circulatum* was separated by nine mutation steps from the three other Palaearctic taxa, *cyathigerum* (*s. str.*), '*risi*' and *deserti*. The only specimen of *deserti* analysed, from Algeria, was closest, as separated by just one mutation step, to a specimen of '*risi*' from Kazakhstan, while two other '*risi*'-haplotypes, separated by two mutation steps, formed the core of the network, from which different haplotypes of *cyathigerum s. str.* differed by 1–2 different substitutions (Turgeon *et al.* 2005: fig. 4a). A multi-locus molecular phylogenetic analysis by Callahan & McPeek (2016) showed that *E. cyathigerum* (s. str.), '*E. risi*', *E. deserti*, and *E. circulatum* in all trees formed a tight monophyletic cluster (clade A), which radiated no earlier than the Late Pleistocene. Thus, the existing molecular data, first by Turgeon *et al.* (2005), in fact provide evidence against (!) species delimitation between *deserti*, *risi* and *cyathigerum*.

Therefore, the original name and subspecific rank of *rotundatum* should be retained:

***Enallagma cyathigerum rotundatum* Bartenef, 1929, valid name**

Distribution: West Caucasus, the steppe zone of European Russia, South Ural, the steppe and forest-steppe zones of Siberia excluding taiga mountains, southern Amur basin, Central Asia south-east to eastern Afghanistan, and to the East at least to Mongolia, probably north-east China. The actual range boundary is still unknown. An isolate may also exist in Central Anatolia (St. Quentin 1964).

Importantly, the molecular data by Turgeon *et al.* (2005) and Callahan & McPeek (2016) provide evidence against the species status of *E. deserti* as well. Morphologically, because of the *boreale*-type cerci as well as by the AFLP data by Turgeon *et al.* (2005), it is much closer to *E. cyathigerum rotundatum* than to *E. cyathigerum cyathigerum*. Moreover, the shift of the yellow lobe of the cercus towards the terminal black tooth in *deserti*, as compared to *rotundatum*, is in the direction which would further lead to the cercus structure of *E. cyathigerum cyathigerum*, if the lobe would protrude caudad from the tooth.

Based on these arguments, I consider it necessary to downgrade *deserti* to subspecies rank:
***Enallagma cyathigerum deserti* (Selys, 1871), stat. rev.**

The following biogeographical hypothesis may be suggested: *Enallagma* individuals with *boreale*-type cerci are distributed from Morocco to Tunisia and then continuously from the West Caucasus to southern Khabarovskiy Kray in the Russian Far East. The limited and unillustrated data of St. Quentin (1964) may indicate that an isolate of such damselflies may exist in Central Anatolia as well. In view of, *e.g.*, the existence of Amphipalaearctic species in birds and butterflies and species with large range disjunctions of other types (Dubatolov & Kosterin 2000), the huge gap between Tunisia and the West Caucasus could be quite recent. The Palaearctic clade of the genus *Enallagma* has been estimated to radiate no earlier than the Late Pleistocene (Callahan & McPeek 2016), so the said gap could appear because of some intrusion of more cold-tolerant *E. cyathigerum s. str.* to the East Caucasus and Asia Minor and perhaps to South Europe during the last Pleistocene cooling. Curiously, *E. cyathigerum s. str.* was also discovered in the Middle Atlas Mts in Morocco (Lohmann 1990) and is also considered to be a

glacial relic there (Jacquemin & Boudot 1999). A similar supposition has already been put forward by St. Quentin (1965b), who termed *E. deserti*, *E. cyathigerum rotundatum*, *E. risi* and *E. circulatum* 'Randformen' (fringe forms). He acknowledged their great similarity but did not challenge their status as different taxa; however, he no longer mentioned his *E. strouhali*, obviously having recognised its synonymy with *E. risi*.

In fact, available molecular data on the Eurasian species with the *boreale*-type cerci (Turgeon *et al.* 2005; Callagan & McPeek 2016) supported only *E. circulatum* as a species separate from *E. cyathigerum* in the broad sense of this paper, including subspecies *deserti* and *rotundatum*, as supposed by May (1997) and Paulson *et al.* (1998). *Enallagma circulatum* differs from *E. cyathigerum deserti* and *E. cyathigerum rotundatum* morphologically (Seidenbusch 1997; Paulson 1998) and has a profound trend of melanisation, with lateral black stripes on the abdomen being widespread.

Such stripes, variable and usually irregular, often appear in *E. cyathigerum cyathigerum* in boggy and taiga habitats from Fennoscandia (J.-P. Boudot pers. comm.) through Siberia to the Far East (Belyshev 1973; Dumont *et al.* 2005; Bernard & Kosterin 2010; Kosterin & Zaika 2010, 2011; Dijkstra *et al.* 2020) and even in Central Europe, *e.g.*, in bogs (R. Jödicke pers. comm.). Several species-group names have been proposed for such individuals from the Far East of Russia by A.N. Bartenev and B.F. Belyshev, all being synonyms. Their complicated taxonomic status will be considered elsewhere. It is noteworthy that such melanisation is unknown in *E. cyathigerum rotundatum*.

Taxonomic status of *Aeshna juncea atshischgho*

The seven syntypes of *Aeschna juncea* var. *atshischgho*, now most probably lost, were the only specimens of *A. juncea* from the Caucasus that Belevich (2005) had at her disposal for the revision of *A. juncea*. She claimed that in the four female syntypes she examined she did not observe the two important morphological diagnostic characters of *A. juncea atshischgho* given by Bartenef (1929b), namely the 'lateral genital plates' and the shallow incision of the vulvar scale. The appendix to her thesis (Belevich 2005: 280) includes drawings of the ovipositor of three of those syntypes, showing no 'lateral genital plates' and the variably but well incised vulvar scale. Curiously, the

'lateral genital plates' were shown, in one drawing in page 282, for three of 12 females of *A. juncea* from Buryatia. Nevertheless, I cannot exclude the possibility that she overlooked those small lobes in Bartenev's female specimens. Belevich admitted a great variability in the vulvar scale as well as the colour pattern and other characters throughout the range of *A. juncea* and doubted

Figure 7. Teneral female of *Aeshna juncea* in life (the same specimen as in Fig. 8a). Russia, West Caucasus, Republic of Adygea, Lagonaki Plateau, a small permanent pool amidst subalpine meadows at the north-eastern foot of Mt Oshten. Photo: OEK (12.vii.2008)

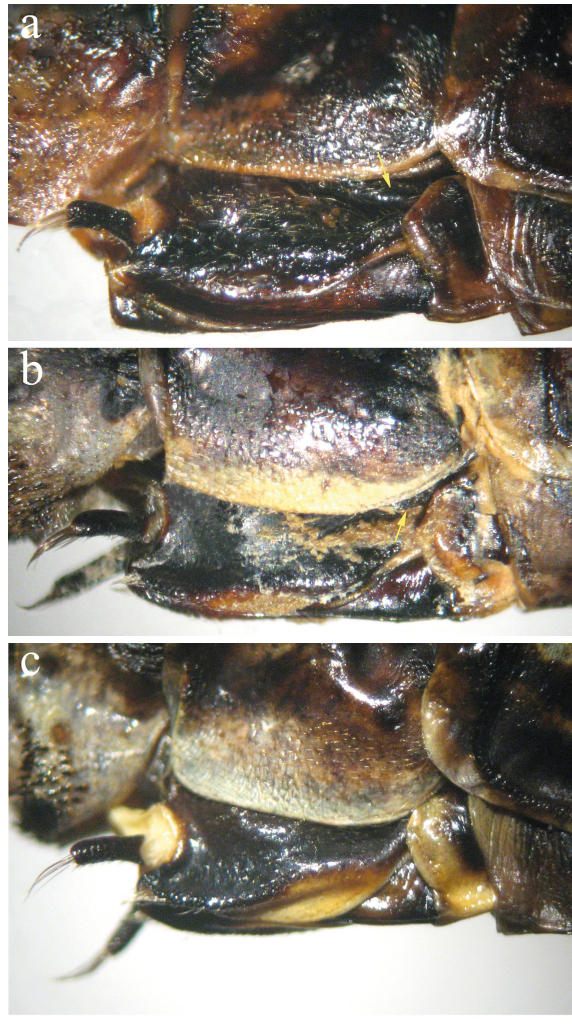

Figure 8. Ovipositor (latero-ventral view) of *Aeshna juncea* females from the Caucasus: a – Russia, West Caucasus, Republic of Adygea, Lagonaki Plateau, small pool at the north-eastern foot of Mt Oshten, 12.vii.2008, leg. OEK; b – Russia, central North Caucasus, Krachay-Cherkes Republic, Zelenchuk District, 7 km south-west of Nizhniy Arkhyz, Lake Taza-Kel' (Forelevoe), 03.vii.2019, leg. V. Onishko & OEK; c – Russia, East Caucasus, Republic of Dagestan, Agul District, Lake Chirag near Chirag village, 18.vii.2021, leg. E.V. Ilyina. The lateral sclerites ('lateral genital plates') of the S9 sternite are indicated with yellow arrows. Scale bar 1 mm.

the existence of any subspecies in *A. juncea.* Therefore, she synonymised all infraspecific taxa with the nominotypical one (conclusion 2 of her thesis).

I failed to get topotypes of *A. j. atshischgho.* However, I managed to collect a teneral *A. juncea* female in West Caucasus, on the Lagonaki Plateau, just *ca* 36 km north-west from the type locality of *atshischgho*, although formally on the opposite, European side of the Great Caucasus. It had large lateral thoracic stripes (Fig. 7), thus conforming the original description of *A. j. atshischgho*, although this character is by no means unique and occurs in this species elsewhere. The vulvar lamina cannot be examined in ventral view since the abdomen of that specimen, collected in teneral condition, was strongly appressed from the sides. Most importantly, it does have short lateral sclerites of S9, 'lateral genital plates' *sensu* Walker (1912) (Fig. 8a). I also have at my disposal females from two localities in the Russian part of the Caucasus. The female from Lake Taza-Kel', Karachay-Cherkes Republic, which is the central part of the northern principal slope of the Caucasus, also has the 'lateral genital plates', although even shorter (Fig. 8b). At the same time, none of the females from Lake Chirag Dagestan, East Caucasus, have these plates (Fig. 8c). Of course, much more specimens of *A. juncea* from the Caucasus would be necessary for even a preliminary inference. However, the fact of presence of the 'lateral genital plates' in females from West Caucasus and in the only available female from Central North Caucasus *versus* their absence in the available females from East Caucasus suggests that the two Caucasian subspecies, *A. j. atshischgho* (with plates) and *A. j. crenatoides* (without plates) proposed by Bartenev may be valid. In view of the extreme shortage of specimens from the Caucasus available for analysis, I cannot make a firm conclusion and retain the taxonomic situation with the Caucasian *A. juncea* unchanged and unresolved. Further studies are necessary to decide if *A. j. atshischgho* is a distinct subspecies or a synonym of *A. j. crenatoides*.

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